NeoBiota 53: 25–39 (2019)
doi: 10.3897/neobiota.53.37431
http://neobiota.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
NeoBiota
Advancing research on alien species and biological invasions

Native generalist consumers interact strongly with seeds of the invasive wild cucumber (*Echinocystis lobata*)

Łukasz Dylewski[1,2], Łukasz Myczko[1], Dean E. Pearson[3,4]

1 *Poznań University of Life Sciences, Institute of Zoology, Wojska Polskiego 71C, Poznań 60-625, Poland* **2** *Institute of Dendrology, Polish Academy of Sciences, Parkowa 5, 62-035 Kórnik, Poland* **3** *Rocky Mountain Research Station, U.S.D.A. Forest Service, Missoula, MT 59801, USA* **4** *Division of Biological Sciences, University of Montana, Missoula, MT 59812, USA*

Corresponding author: *Łukasz Dylewski* (ldylewski@man.poznan.pl)

Academic editor: *J. Kollmann* | Received 17 June 2019 | Accepted 12 November 2019 | Published 29 November 2019

Citation: Dylewski Ł, Myczko Ł, Pearson DE (2019) Native generalist consumers interact strongly with seeds of the invasive wild cucumber (*Echinocystis lobata*). NeoBiota 53: 25–39. https://doi.org/10.3897/neobiota.53.37431

Abstract

When alien plant species arrive in a new environment, they develop novel interactions with native biota that can range from negative to positive. Determining the nature and strength of these interactions is integral to understanding why some aliens are suppressed and others become highly invasive pests. For introduced terrestrial plants, seed and seedling interactions with native biota are crucial, because most nascent populations start from seed. Herein, we explored interactions between native generalist rodent and bird consumers and seeds of the invasive wild cucumber *Echinocystis lobata* by conducting seed-offering experiments in Poland. We also evaluated how interspecific competition from native plants and intraspecific competition from clustering of *E. lobata* seed (clustering resembling consumer seed caching) affected survival of seedlings and young plants. Native consumers interacted strongly with *E. lobata* seeds, with rodents removing 98% of seeds from ground locations and birds removing 24% of elevated seeds. Camera and live traps indicated that striped field mice *Apodemus agrarius* were the predominant rodent removing seeds. Camera traps and visual observations indicated that great tits *Parus major* and European jays *Garrulus glandarius* were the primary bird species removing elevated seeds. While some level of seed removal was likely attributable to seed predation, as indicated by seed coat remains, we also observed evidence that rodents may cache *E. lobata* seeds and *Garrulus glandarius* are known to cache and disperse seeds. Monitoring of seedlings indicated that increasing cover of native plants and clustering of *E. lobata* seedlings both reduced survival of seedlings and young plants due to inter- and intraspecific competition, respectively. Hence, caching by generalist consumers may disperse *E. lobata* seeds, which are heavy and lack dispersal adaptations, but such caching may also reduce individual seedling survival rates. Fully understanding invasion success of the *E. lobata* will require evaluating the net effects of generalist consumers on its recruitment and dispersal.

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Keywords
biotic resistance, corvid, competition, *Echinocystis lobata*, rodents, seedling survival, seed predation, seed dispersal

Introduction

Understanding why some introduced plant species become problematic invaders, while others are naturalised residents, is a primary question motivating invasion ecology (Pyšek et al. 2012; Pearson et al. 2018). Successful establishment of an invader indicates that abiotic conditions are at least sufficient to support its fundamental niche requirements (Hutchinson 1957), suggesting an important role of biotic factors in defining the invader's realised niche and ultimate success (Elton 1958; Maron and Vilà 2001; Levine et al. 2004). Many biotic components of the recipient community will establish a variety of novel interactions with the invader, which may range from strongly negative to strongly positive (Mack et al. 2000; Keane and Crawley 2002; Parker et al. 2006). Determining the nature and strength of these interactions is crucial for understanding invader success.

Most terrestrial plant invaders establish nascent populations from seed. Therefore, seed survival, dispersal and seedling establishment are particularly critical processes determining the success of newly introduced plants (Colautti et al. 2006; Kleunen et al. 2018). Accumulating evidence suggests that post-dispersal seed predation by generalist consumers is a strong ecological filter affecting recruitment of both native and introduced plants (Reader 1993; Larios et al. 2017; Maron et al. 2012). Mounting evidence indicates that rodent seed predators have particularly strong effects on the establishment success of introduced plants (Reader 1993; Pearson et al. 2011; Maron et al. 2012). Granivorous birds and ants may also influence introduced plant success (Nuñez et al. 2008; Pearson et al. 2014), but far less is known about how these interactions, mediated by these consumers, affect recruitment of alien or native plants.

Generalist consumers may function as effective seed predators when they destructively consume seeds (Janzen 1971), but they also act as seed dispersers when they cache seeds for later consumption that they fail to retrieve and consume (Vander Wall 1993; Gómez et al. 2018). In this capacity, some birds may serve as important agents of seed dispersal, particularly long-distance dispersal, for both native and exotic plants (Richardson et al. 2000; Myczko et al. 2014). Rodents may similarly disperse seed through caching behaviour, but the dispersal distances tend to be much shorter (Ribble 1992; Iida 1996). The overall importance of seed dispersal via caching is not well understood, because it is logistically challenging to locate cached seeds to determine seed fates (but see Xiao et al. 2015; Bogdziewicz et al. 2018; Wróbel and Zwolak 2019). Importantly, when forgotten caches do germinate, the benefits to germinating seedlings are not always clear, because caching can result in high seedling densities, high competition and low survival (Howe 1989; Lambers et al. 2002; Kurek et al. 2018). In short, mounting evidence suggests that generalist granivores play important roles in

plant establishment that strongly influence plant invasion, while the balance between seed destruction and dispersal is poorly understood, even for native plants.

Herein, we quantified interactions between native generalist rodent and bird consumers and seeds of the introduced *Echinocystis lobata* in Poland, where this plant is invasive. We conducted seed-offering studies to quantify seed removal rates for both consumer guilds and identified species removing seeds via trapping, remote cameras and visual observations. We also quantified survival of naturally occurring solitary and clustered seedlings to understand how interspecific competition from native plants and intraspecific competition of the sort that might arise from consumer seed caching behaviour might affect seedling survival.

Methods

Study area

The seed removal experiments were conducted in October and November 2016 in four study sites located in two study areas in the Wielkopolska province of Poland: Noteć 1 (53°03'N, 16°52'E), Noteć 2 (53°01'N, 16°54'E), Kanał Grabarski 1 (52°10'N, 16°28'E) and Kanał Grabarski 2 (52°08'N, 16°28'E). The distance between the Noteć and Kanał Grabarski study areas was 96 km. The distance between Noteć 1 and Noteć 2 was 3.4 km and that between Kanał Grabarski 1 and Kanał Grabarski 2 was 2.5 km. Each study site consisted of a strip of typical riparian vegetation ≥ 1 km where *Echinocystis lobata* occurred and that was characterised by *Alnus glutinosa*, *Anthriscus sylvestris*, *Bromus inermis*, *Calystegia sepium*, *Fraxinus excelsior*, *Galium aparine*, *Glyceria maxima*, *Humulus lupulus*, *Phragmites australis*, *Poa palustris*, *Sambucus nigra*, *Symphytum officinale* and *Urtica dioica*.

Study species

Echinocystis lobata is native to central North America from the east coast to the Rocky Mountains where it is associated with a broad range of riparian habitats, including stream, river and lake side areas (Foster and Duke 1990). This species was introduced to Europe at the end of the nineteenth and the beginning of the twentieth century as an ornamental plant (Tokarska-Guzik 2005). *Echinocystis lobata* is listed as one of the 100 most invasive alien species threatening natural ecosystems in Europe (Nentwig 2009), where it invades riparian communities (e.g. rushes, riparian forests and nitrophilous habitats). *Echinocystis lobata* can overgrow native herbaceous plants and it competes as well with native vine species, such as *Calystegia sepium* and *Humulus lupulus* (Tokarska-Guzik 2005).

Echinocystis lobata is an annual vine in the gourd family (Cucurbitaceae). It produces fleshy fruits 2.5–5.0 cm long and 2.5–3.5 cm wide that are covered by spines.

We have observed little consumption of the fruits in the introduced range (LD and LM, pers. observ.). Typically, fruits produce four seeds that dehisce at the end of the growing season, with the dried fruit remaining attached to the plant and the seeds falling to the ground. Hence, the diaspores overwinter as seeds not as fruits and are thus exposed to seed predators.

The seeds of the species are large (mean seed mass = 0.33 g; length = 17 mm; width = 8 mm; Dylewski et al. 2018) and smooth, lacking any specific adaptations for dispersal. Recruitment mostly occurs as single individuals, but also appears as loose aggregations of 2–4 seedlings or dense clusters, ranging up to 31 seedlings (Fig. 1). Since fruits commonly produce 3–4 seeds, loose aggregations are attributed to entire fruits falling to the ground. Dense clusters of large numbers of seedlings suggest caching by vertebrates, though this is difficult to confirm.

Seed removal

We conducted seed removal experiments at ten stations at each study site, with each station separated by at least 100 m. We placed two green circular plastic trays (25 cm diam.) at each station (one for small rodents and one for birds) in the immediate vicinity of adult *E. lobata* individuals (< 1.5 m). The trays for small rodents were placed on the ground and covered with 4-cm wire mesh cages (30 cm × 30 cm × 15 cm height with two holes cut 8 cm × 8 cm) to minimise bird access to seeds (cameras observed no birds at these trays – see Results). The trays for birds were placed on top of wooden posts 1.5 m above the ground which protected seeds from mice and voles (cameras observed no voles or mice at these trays). We placed 20 *E. lobata* seeds in each tray (only seeds no fruits). We visited the trays each day for 5 days after initiation of the experiments to record the number of *E. lobata* seeds remaining.

To identify small rodent species potentially removing seeds, we established two live traps (TRIXIE TX-4192, size 5 cm × 5 cm × 17 cm) near each tray and at the central point between tray locations after seed removal experiments were complete. We trapped rodents for 24 h at each location four times over the course of the season, using *E. lobata* seeds as bait. During each visit, we surveyed each elevated tray from 30-m distance for 5 min to identify bird species removing seeds. Additionally, we set out two camera traps during the experiment at one randomly selected station at each study site, such that one camera was located next to a rodent tray and one next to a bird tray (four camera traps in Kanał Grabarski research area and four camera traps in Noteć research area).

Seedling survival

To evaluate how seed dispersion and native plant abundance influenced seedling survival, we located thirty 2 m × 8 m plots containing naturally occurring seedlings (≥ 50 m apart) at two study sites (15 at Kanał Grabarski 1 and 15 at Kanał Grabarski 2)

Figure 1. Seedlings of *E. lobata* most commonly occur as **a** single individuals but also can be found in **b** tight clusters, suggesting seed caches.

to follow seedling fates over time. Our primary interest was to evaluate how single vs. clustered seedlings affected seedling survival in an effort to understand how caching activities might influence seedling success. Accordingly, each plot was selected to include one cluster of aggregated *E. lobata* seedlings and four isolated seedlings. Since *E. lobata* seedlings sometimes occur in aggregations of 3–4 due to seeds being collocated with fallen fruits, we focused on aggregations that contained five or more adjacent seedlings which could plausibly represent rodent caches (see Fig. 1a). Within each plot, we established one 1-m diameter circular subplot centred on each seedling and seedling cluster. Upon initiation of each subplot, we removed any additional *E. lobata* seedlings within the subplot and estimated cover of grasses, herbaceous plants and *Urtica dioica* therein. We visited each plot every 7 days (nine total visits per plot) and recorded survival of *E. lobata* seedlings and young plants.

Statistical analysis

We applied survival analysis to examine seed removal using life tables (Kleinbaum 1996). In this analysis, survival is analogous to seeds remaining over the course of exposure to consumers (i.e. the probability of escaping seed removal) and is not intended to infer seed fate beyond removal. The interval for obtaining estimates was 5 days from the start to the end of the seed exposure period. To determine how the different factors affected the probability of escaping seed removal, we used Cox's proportional hazards model (Cox 1972) as applied by Myczko et al. (2014) to bird predation on acorns. First, we developed a full model examining effects of consumer (rodent or bird), study area (Noteć or Kanał Grabarski) and their interaction: consumer category × study area on the probability of escaping seed removal (Table 1). As both factors and their interaction were significant and there is no option for post-hoc tests for the Cox's proportional hazard analysis, we followed up this analysis with two

Table 1. Results from Cox's proportional hazards analysis for measured factors and interactions potentially influencing the removal of wild cucumber seeds (n = 1600).

Factor	Parameter estimate (β)	SE (β)	χ^2	P	95% CI
Vertebrate type	2.225	0.127	309.3	< 0.001	7.22–11.86
Study area	-0.711	0.163	19.0	< 0.001	0.36–0.68
Vertebrate type × Study area	0.865	0.179	23.5	< 0.001	1.67–3.37

models examining the effects of rodents and birds on the probability of escaping seed removal by study area separately.

We used the Mann-Whitney U test to compare the number of bird observations and rodent captures between research areas in order to relate consumer abundance to removal rates. We evaluated how seedling dispersion (clustered vs. single seedlings) related to survival of seedlings and young plants using Cox's proportional hazards model. In this model, we also evaluated how the different factors (i.e. seedling density (clustered or single), cover of grasses (dominated by *Phragmites australis*), cover of *Urtica dioica* and cover of other forbs and their interaction: seedling dispersion × cover of grasses, seedling dispersion × cover of grasses, seedling dispersion × cover of other forbs), affected seedling survival (from the initial seedling phase through the young plant phase, up to 63 days). Finally, we used logistic regression as a further test of how seedling number within an aggregation affected the probability of seedling and young plant survival. All analyses were performed using IBM SPSS 21 for Windows (IBM SPSS 2012). All means reported ± SE.

Results

Identification of seed removal agents

Numerous species were observed visiting and removing seeds from *E. lobata* seed offerings. We live-trapped four rodent species in the Noteć area: *Apodemus agrarius* (n = 95), *Myodes glareolus* (n = 6), *Apodemus flavicollis* (n = 3) and *Apodemus sylvaticus* (n = 2). In the Kanał Grabarski area, we live-trapped *Apodemus agrarius* (n = 57), *Myodes glareolus* (n = 26), *Apodemus flavicollis* (n = 2) and *Microtus arvalis* (n = 1). Cameras located at the ground trays generated 202 × 30-sec. movies in the Kanał Grabarski area where we recorded *Apodemus agrarius* (n = 73), *Myodes glareolus* or *Microtus* sp. (n = 26) and *Apodemus flavicollis* or *Apodemus sylvaticus* (n = 11) visiting and/or removing seeds from trays.

In the Noteć area, the cameras generated 268 × 30-sec. movies documenting *Apodemus agrarius* (n = 139) and *Myodes glareolus* or *Microtus* sp. (n = 12) visiting and/or removing seeds from the trays. In both study areas, the cameras indicated that *Apodemus agrarius* were the predominant removers of *E. lobata* seeds. Camera traps at elevated seed trays generated 144 × 30-sec. videos that identified two granivorous bird species removing seeds from trays: the omnivorous *Parus major* (n = 3) and the omnivorous, scatter-hoarding *Garrulus glandarius* (n = 2).

Seed removal

The Cox's proportional hazard analysis for the full model was significant overall ($\chi^2 = 710.9$, df = 3, $p < 0.001$), with consumer category ($\beta = 2.22 \pm 0.13$, $p < 0.001$), study area ($\beta = -0.71 \pm 0.16$, $p < 0.001$) and consumer category × study area interaction ($\beta = 0.87 \pm 0.18$, $p < 0.001$), all significantly influencing the probability of removal of *E. lobata* seeds (Table 1). In the separate models, rodent effects did not differ between research areas ($\chi^2 = 0.57$, df = 1, $p = 0.452$) but bird effects did ($\chi^2 = 19.8$, df = 1, $p < 0.001$). The probability of seeds remaining at the end of the experiment was dramatically lower for seeds accessed by rodents ($\bar{x} = 0.026 \pm 0.000$) than for seeds accessed by birds ($\bar{x} = 0.862 \pm 0.005$), with 92.5% vs. 2.5% of seeds removed in 24 h by rodents versus birds, respectively (Fig. 2).

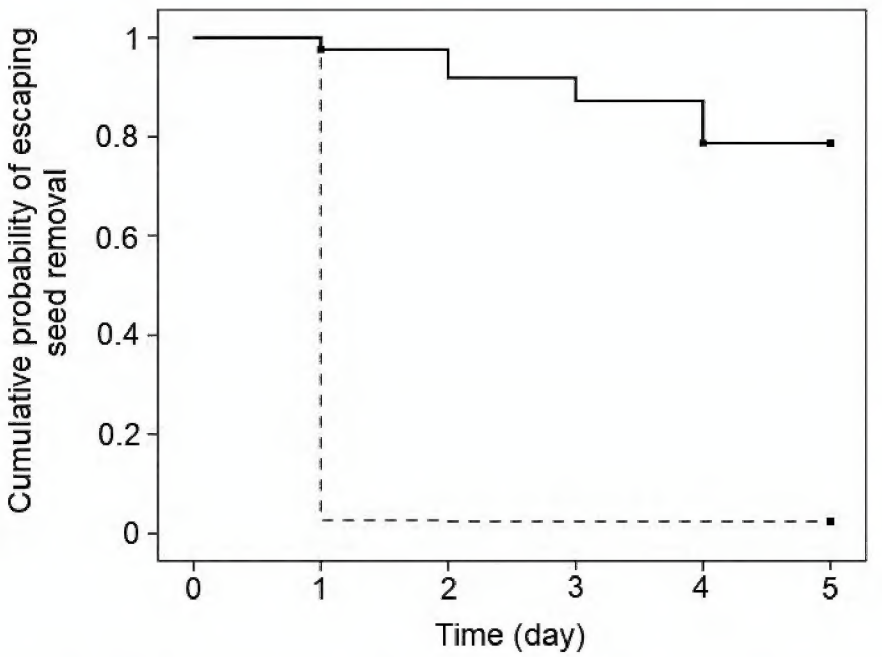

Figure 2. Probability of escaping seed removal (escape curves) for *E. lobata* seeds exposed to bird (solid line) and mammal granivores (dotted line).

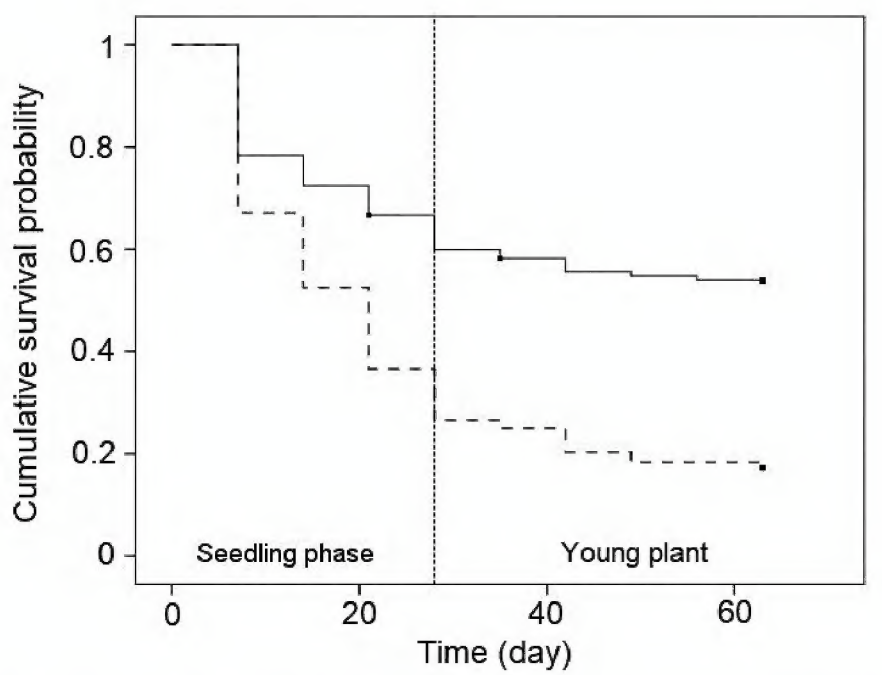

Figure 3. Differences in survival probabilities for *E. lobata* seedlings and young plants for single (solid line) and aggregated seedlings (dotted line).

Table 2. Results from Cox's proportional hazards analysis of factors influencing the survival of wild cucumber seedlings and young plants (n = 421).

Factor	Parameter estimate (β)	SE (β)	χ^2	P	95% CI
Seedling density	0.902	0.156	33.4	< 0.001	1.82–3.35
Cover of grass	-0.374	0.151	6.1	0.013	1.08–1.96
Cover of *Urtica dioica*	-0.443	0.169	6.9	0.009	1.12–2.17
Cover of other forbs	-0.289	0.200	2.1	0.149	0.90–1.98
Seedling density × Cover of grass	-0.231	0.169	1.9	0.172	0.57–1.11
Seedling density × Cover of *Urtica dioica*	-0.328	0.181	3.3	0.070	0.51–1.03
Seedling density × Cover of other forbs	-0.294	0.215	1.6	0.173	0.49–1.14

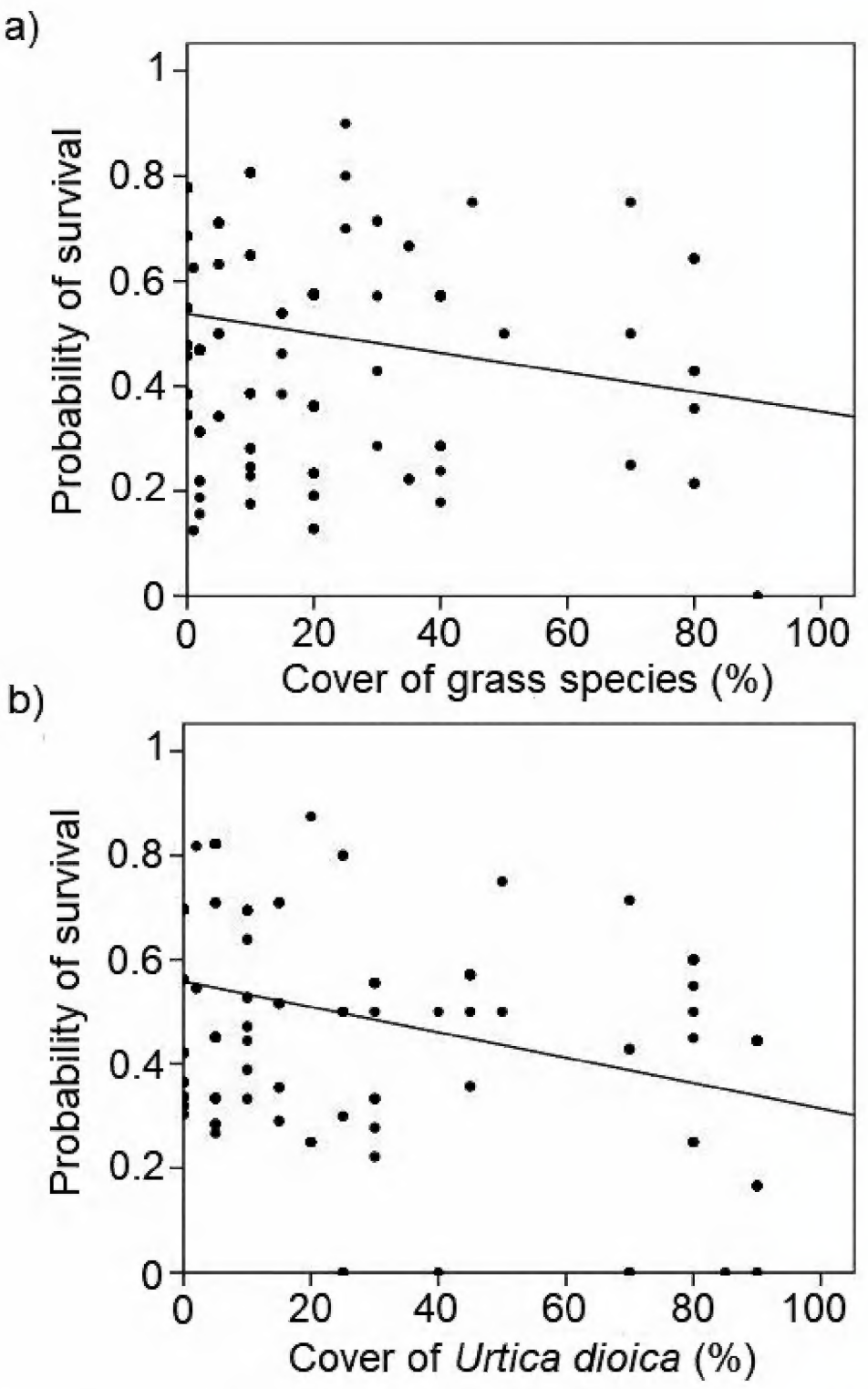

Figure 4. The effects of **a** cover of grass species and **b** cover of *Urtica dioica* on *E. lobata* seedling and young plant survival probabilities.

These results suggest that rodents may be the primary seed removing species. The mean removal rate for seeds over the 5-day period was higher for Noteć ($\bar{x} = 0.907 \pm 0.005$; n = 400) than for Kanał Grabarski ($\bar{x} = 0.804 \pm 0.009$; n = 400). This difference was consistent with the finding of fewer bird observations in the Noteć research area ($\bar{x} = 1.54 \pm 0.35$) compared with the Kanał Grabarski area ($\bar{x} = 4.68 \pm 1.50$) (U Mann-Whitney Z = 2.03, p = 0.042), suggesting that avian activity levels were correlated with avian seed removal rates. Rodent captures did not differ between study areas (U Mann-Whitney Z = 0.315, p = 0.752).

Seedling survival

The mean number of seedlings growing from clusters was 10 ± 4.09 (min–max 5–31).

The Cox's proportional hazard model, including all factors, was significant overall ($\chi^2 = 51.9$, df = 7, $p < 0.001$), with seedling density ($\beta = 0.902 \pm 0.156$, Fig. 3), cover of grass ($\beta = -0.374 \pm 0.151$) and cover of *Urtica dioica* ($\beta = -0.443 \pm 0.169$) significantly influencing *E. lobata* survival (Table 2, Fig. 4), but interactions were all non-significant ($p > 0.05$) (Table 2). Hence, native grasses and *Urtica dioica* appeared to have the ability to reduce seedling survival. The probability of survival of individuals growing in aggregation was $\bar{x} = 0.173 \pm 0.020$, whereas the probability of survival of individuals growing separately was $\bar{x} = 0.542 \pm 0.445$. The logistic regression indicated that the number of seedlings in an aggregation negatively correlated with survival of *E. lobata* plants ($\chi^2 = 6.0$, df = 1, p = 0.014). Collectively, these results suggest that higher densities of *E. lobata* seedlings, such as those arising from apparent seed caching, greatly reduced seedling survival.

Discussion

The success of introduced plants can be strongly influenced by the novel interactions they develop with native species in the recipient range, particularly natural enemies (Keane and Crawley 2002). In this study, we documented strong interactions between native generalist rodent and bird consumers and the invasive *E. lobata*. Our seed-offering experiments demonstrated that, after only 5 days, rodents and birds had removed 97.6% and 23.8% of *E. lobata* seeds, respectively. While we could not determine the fate of removed seeds in our study, these high seed removal rates suggest that *E. lobata* seeds may experience high levels of consumption by generalist omnivores. However, we also observed evidence that rodents may cache *E. lobata* seeds and *Garrulus glandarius* are known to disperse seed via scatter hoarding, suggesting that these consumers may have both positive and negative effects on this introduced plant.

Echinocystis lobata seeds set out in ground depots were quickly depleted by consumers. Both live traps and camera traps suggested that the primary seed removers were rodents, particularly *Apodemus agrarius*. While birds could possibly have removed

some of these seeds, these depots were covered by wire cages to limit bird access and no birds were captured in live traps baited with cucumber seeds or observed by camera traps at these stations. *Apodemus agrarius* are formidable seed predators (Babińska-Werka 1981; Brown et al. 2007; Baraibar et al. 2009) and empty seed coats located at the ground depots and trays suggested that many seeds were consumed on site. However, these mice may store the seeds in caches (Zhang et al. 2016) and we found dense clusters of *E. lobata* seedlings that were strongly suggestive of rodent seed caches, while *E. lobata* seedlings may sometimes be clustered due to fruits falling before seeds dehisce (see above). The prospective caches we observed were often comprised of 1–2 dozen seedlings emerging in tight bundles, suggesting aggregated burials (Fig. 1).

In following seedling clusters over time, we found that survival of clustered seedlings was much lower than that of the more commonly observed dispersed seedlings, indicative of natural seed dispersal for this plant. Furthermore, increasing seedling density within clusters was correlated with reduced survival, suggesting a role of intraspecific competition, consistent with McMurray et al. (1997). While some seeds removed by rodents may be cached and dispersed over short distances, the clustering associated with cached seeds may reduce individual seedling survival rates (Lambers et al. 2002; Lu et al. 2015; Kurek et al. 2018). Overall, *E. lobata* seeds located on the ground experienced very high removal rates, suggesting rodent seed predation.

In contrast to seeds located on the ground, *E. lobata* seeds set out on elevated trays experienced much lower removal rates. Nonetheless, seed removal at these trays was still substantial, with almost 25% of the seed removed in 5 days. Visual observations conducted at all of the trays and cameras placed at a subset of the trays identified *Parus major* and *Garrulus glandarius* as primary removers of these seeds – both species are important seed predators (Bossema 1979; Sherry 1989). However, *Garrulus glandarius* are also scatter hoarders that serve as an important long-distance dispersal agent for several deciduous tree species (Bossema 1979; Pons and Pausas 2007). This species may carry seeds (especially acorns and other nuts) from 250 m to 5 km to storage sites (Vander Wall 1990; Gómez 2003). In temperate forests, *Garrulus glandarius* are an important dispersal vector of invasive *Quercus rubra*, contributing to its colonisation of new areas (Myczko et al. 2014). Our results suggest that birds may act as seed predators and also possibly important dispersers of *E. lobata* seed in the invaded region in Poland.

Competition with native plants is another important source of biotic resistance to alien plant seedling establishment (MacDougall and Turkington 2005; Dylewski et al. 2017). In monitoring seedling survival, we found that higher cover of dominant grass species and *Urtica dioica* was linked to higher seedling mortality. As a vine, *E. lobata*'s success as an invasive species is contingent upon growing tall enough to overtop other plants. Therefore, locations with lower competition from native plants, combined with lower seed predation, may be most susceptible to *E. lobata* invasion.

Introduced plants may interact with native consumers in a variety of ways that can influence plant invasion and alter native consumer abundance and behaviour. Many studies have shown that native rodent, bird and insect consumers will remove the seeds of introduced plants (e.g. Folgarait and Sala 2002; Nuñez et al. 2008; Carrillo-Gavilán

et al. 2010; Pearson et al. 2014). Fewer studies have taken the next step to demonstrate that native seed predators can suppress the establishment of introduced plants (Reader 1993; Pearson et al. 2011; Maron et al. 2012; Connolly et al. 2014), while others have shown that native consumers may serve as important dispersers that facilitate invasion (Lenda et al. 2012; Myczko et al. 2014; Wróbel and Zwolak 2019). Reciprocally, introduced plants may alter the abundance and behaviour of native consumers via food subsidies, apparent competition and habitat changes (Pearson and Fletcher 2008; Pearson 2009; Mattos and Orrock 2010; Guiden and Orrock 2017).

Our results suggest that, within this system, native consumers may both strongly reduce *E. lobata* seed availability, which could reduce local *E. lobata* densities and also facilitate its dispersal to new locations. In turn, the high production of large, palatable seeds could subsidise native consumer populations with a range of indirect effects. While our seed-offering studies were not designed to determine the outcomes of these interactions and our sampling was limited in space and time, our results do suggest that strong interactions are taking place between this annual invader and native consumers that could influence both *E. lobata* invasion and its effects on native communities within its introduced range in Poland.

Acknowledgements

We thank the editor and two anonymous reviewers for helpful comments on the manuscript. We would like to acknowledge Jacek Więckowski, Kacper Więckowski and Aleksandra Kraśkiewicz for their assistance in rodent capture field work. This project was supported by the National Science Centre, Poland, under the fellowship "Etiuda" no. 2018/28/T/NZ8/00264 for ŁD.

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